# SYMBIOTIC RELATIONSHIPS BETWEEN ECTOPROCTS AND GASTROPODS, AND ECTOPROCTS AND HERMIT CRABS IN THE FRENCH JURASSIC

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ABSTRACT. Certain gastropods from the Pierre Blanche de Langrune (Upper Bathonian) at Lion-sur-Mer, Calvados, France, have been encrusted by a succession of ectoproct zoaria. After the death of the gastropods, the vacated shells, with their encrustations, have been occupied by hermit crabs. Abrasion of the shell during locomotion of the crabs produces flat areas near the shell aperture, and discontinuities in the ectoproct colony growth. The relationship between the ectoproct and the inhabitant of the shell is considered to be one of true symbiosis.

IN the course of work by one of us (T.J.P.) on the palaeoecology of Upper Bathonian faunas in England and northern France, collections were made from the upper caillasse (= shell bed) within the Pierre Blanche de Langrune (*Clydoniceras discus* Zone), exposed on the foreshore at Lion-sur-Mer, Calvados. The caillasse rests on a hardground 9 m beneath the top of the Pierre Blanche. Among the more striking objects to be found in this bed are colonies of encrusting ectoprocta, whose over-all shapes approximate to that of a trochiform gastropod. These colonies are relatively common, and it is a feature of all of them that part of the colony, usually next to the aperture, is worn flat (Pl. 65, fig. 1). A section through the colony confirms the opinion that it has been built up by successive layers of ectoproct, of the genus *Berenicea*, growing on a gastropod shell (probably *Ataphrus* sp.) (Pl. 65, figs. 2, 3).

We postulate that the following sequence of events has given rise to the objects as we find them in the caillasse:

1. In certain, but not all, of the colonies, colonization by the ectoproct has started before the completion of growth of the gastropod. In these cases, the outer whorl of the shell may be seen to enclose a layer or two of the ectoproct zoaria between itself and the adjacent inner whorl (Pl. 65, fig. 4). Whilst the gastropod is alive, the shell is supported by the foot during locomotion. In this event, the whole of the upper surface of the shell is available for colonization by the ectoproct, and none of the shell is being dragged along the substrate and abraded. The first few layers of zoaria thus cover the shell uniformly (Pl. 65, fig. 3).

2. After the death of the gastropod, the shell is occupied by a hermit crab. No longer being supported by a fleshy foot, it is dragged along the substrate. Any zoaria covering the area of contact with the substrate are worn off, whilst growing zoaria are prevented from expanding to cover this area. Therefore the subsequent layers grow asymmetrically around the shell, and the area in contact with the substrate remains flat (Pl. 65, figs. 3, 5). Even when the crab retracts into the shell, the shell rests on the flat area, and is therefore not available as substrate to the spreading ectoproct.

3. The layers of zoaria continue to accrue whilst the shell is inhabited by the hermit crab, or, more likely, a succession of hermit crabs. The crabs have therefore to main-

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tain for themselves an opening from the shell to the outside. The genetic programme for the shell aperture to be laid down in a trochospiral arrangement has been lost with the death of the gastropod. Therefore the aperture maintained by the pagurid leads straight to the outside (Pl. 65, fig. 5), rather than spirally, as when the gastropod was alive.

4. The colony now grows only by addition of successive layers of ectoproct zoaria over the surface, and not according to a trochospiral pattern as when the gastropod was alive. These zoaria tend to round off the angulations of the trochiform shell, and the shape of the colony changes from being dominantly conical to dominantly ovoid. This effect is enhanced by the continued abrasion on one side (compare the over-all shape of the colony in Pl. 65, fig. 5 with that of the original gastropod). This change in shape results in a change in the location of the area which is dragged along the substrate, and consequently in the stable resting position of the colony when the crab is withdrawn into the shell, from the base of the trochospire to the long side of the ovoid, where the convexity is least. A section through the colony shows how the flattened area migrates with successive layers of zoaria as the over-all shape of the colony changes from coniform to ovoid (Pl. 65, fig. 6).

## DISCUSSION AND CONCLUSIONS

Of the twenty-six examples of the encrusted gastropods collected by the authors from this bed (Oxford University Museum catalogue numbers J. 40001–40026), all but one show the pagurid wear marks, and in none is the hole which allowed emergence of the crab overgrown by ectoprocts. It would seem, then, that demand for housing by pagurids was high, and that only very seldom did a dwelling remain vacant for any significant period of time. Such a conclusion is in keeping with observations made independently by the two authors, in the Canary Islands (C.D.H.), and off the Florida Keys (T.J.P.), that empty gastropod shells are virtually never found on the sea bottom. Either they contain a gastropod, or they contain a hermit crab. Considering that the crabs rely on being able to change their shells each time that

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### EXPLANATION OF PLATE 65

Fig. 1. Colony of ectoproct zoaria encrusting a trochiform gastropod. The lower left corner of the colony has been worn away (arrowed) due to abrasion against the substrate during locomotion of the hermit crab which occupied the shell, OUM, J. 40001, $\times 2{\cdot}2$.

Fig. 2. Section through colony along plane sub-parallel to worn area, showing successive layers of ectoproct zoaria, OUM, J. 40002a, $\times 3{\cdot}0$.

Fig. 3. Section through colony cutting across worn area (arrowed). Encrustation of this specimen started before death of the gastropod (see fig. 4). Consequently, the first few layers of zoaria at the point of wear, are unabraded, OUM, J. 40003a, $\times 2{\cdot}8$.

Fig. 4. Part of fig. 3 showing four layers of zoaria (arrowed) enclosed between the last whorl of the gastropod and the preceding whorl. This indicates that colonization by the ectoproct started whilst the gastropod was still alive, $\times 8{\cdot}0$.

Fig. 5. Section through colony showing the aperture (arrowed) maintained by the hermit crab. It leads to the outside in a straight line, OUM, J. 40004a, $\times 3{\cdot}0$.

Fig. 6. Details of the change in location of the area of abrasion: the arrows point along the planes of contact with the substratum, for successive growth stages of the colony. These planes of contact, where abrasion occurred, change location as the over-all shape of the colony becomes less trochospiral, and more ovoid, OUM, J. 40004b, $\times 4{\cdot}6$.


PALMER and HANCOCK, symbiotic relationships they outgrow their previous one, it seems not unlikely that any change by a larger individual is rapidly followed by the reoccupation of the recently vacated shell by a slightly smaller individual, and so on until one very small shell is vacated and left vacant.

Associations between gastropods, encrusting organisms, and hermit crabs are known from periods other than the Jurassic. Wear marks ascribed to hermit crabs have been described on Recent gastropods encrusted by hydractinians (Schäfer 1962). Similarly worn, but unencrusted, gastropods have been described from the Pliocene of Belgium by Boekschoten (1967), and an unworn example encrusted by the ectoproct *Cellepora* sp., from the Pliocene of Britain, has been figured by Pinna (1972, p. 33).

Busk (1857, pl. 9, fig. 6*c*) also figures *Cellepora edax* Busk encrusting a gastropod, and Wood (1872, p. 55) discusses the encrustation of *Turritella crassicostata* by *Edax*. The Oxford University Museum Pleistocene collection contains five specimens showing wear marks on gastropod shells encrusted by hydractinians (OUM, Q. 1512–1516); there is also a *Natica* sp. from the Coralline Crag (Pliocene), which is encrusted by *Cellepora edax* and similarly worn.

Busk (loc. cit.) considers that *Cellepora* was parasitic upon the gastropod shell, since it frequently appears, both in Pliocene and Recent examples, to have effected the solution of the underlying shell. However, in these examples there is no evidence that there was any occupant of the shell at the time during which the solution occurred, and the inference of a parasitic relationship is not justified. In the Bathonian specimens, the ectoproct colony was both active and growing during the life of the gastropod, as well as during the subsequent occupation of the shell by the hermit crab. In this case, there was no destruction of the shell by the ectoproct, and the relationship between gastropod and ectoproct would appear to have been one of true symbiosis. The shell provides a stable substrate, and the behaviour of the gastropod prevents it constantly being rolled around and abraded by current activity. In turn, the ectoproct offers the gastropod protection by disguise, and it also strengthens the shell against attack by mollusc-eating vertebrates and predatory decapods. This reasoning applies equally if the shell is occupied by a hermit crab; in this case, however, the ectoproct probably gains further by gathering food particles released by the scavenging behaviour of the crab, as well as those suspended in the crab's respiratory currents.

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*Note added in press*. Further discussion, particularly on the identity of the ectoproct, may be found in: Fischer, J.-C. and Buge, E. 1970. *Atractosoecia incrustans* (d'Orbigny) (Bryozoa Cyclostomata) espèce bathonienne symbiotique d'un Pagure. *Bull. Soc. géol. France*, **12**, 126–133.